The biology, behaviour, and ecology of *Mastomys natalensis* in southern Africa

CORNELIUS G. COETZEE [1]

The multimammate mouse, Mastomys natalensis, *is the most widespread and common rodent in Africa south of the Sahara. It is an ideal carrier of normally non-human diseases to the domestic environment, not only because of its semi-commensal habit but also because of a combination of other behavioural and ecological factors. Of these, the most important is an exceptionally high propagation rate.*

INTRODUCTION

The multimmate mouse, *Mastomys natalensis* (A. Smith, 1834), is the most widespread rodent in Africa, occurring from Knysna on the southern coast to Eritrea in the north-east and Morocco in the north-west. It is absent from the following places: the extremely moist areas of the Zaire-basin; montane forests; the dry parts of the Karoo, Kalahari, north-western Cape and southern parts of South-West Africa, the Namib areas, Sahara and Somali deserts; and typical winter rainfall areas. Climatic conditions in the different parts of the range of the multimammate mouse vary remarkably. The range includes open grassland, mixed savannah, and clearings in West African forests. The mouse is present in areas where frost occurs over 90 days per year, with a mean annual rainfall of less than 400 mm, and in areas where the mean minimum temperature is 23°C and precipitation 4 000 mm per annum.

The multimammate mouse is thus extremely adaptable and one would expect to find variation in its basic ecology and behaviour. Throughout its range a common factor is found: when one compares the population density in the open bush with that around human habitations, the latter is normally higher. This semicommensal habit is of prior importance in the spread of disease.

In this paper, the emphasis is on factors that might have an influence on population growth and explosion. In the epidemiology of a zoonotic disease (or a potential one such as Lassa fever) the period of high rodent density is of the greatest importance.

[1] Director, State Museum, Windhoek 9100, Namibia.

TAXONOMIC STATUS OF *MASTOMYS* THOMAS, 1915

Prior to the introduction of the generic name *Mastomys* by Thomas in 1915, the multimammate mouse was grouped with *Mus*, *Epimys*, or *Rattus*. This indicates that it holds an intermediate position between the house mouse and the ship (roof) rat. Davis, in Davis & Oettlé (9), compared the characters of these genera and in 1965 Davis (8) grouped *Mastomys*, *Myomys*, *Myomyscus*, and *Hylomyscus* as subgenera of *Praomys*. Some workers (19, 21) are still in favour of maintaining *Mastomys* as a genus. However, it also appears that the name *Mastomys* has become a vernacular name for the multimammate mouse. It is generally accepted that all the previously described species of *Mastomys* are conspecific, e.g., *erythroleucus* and *coucha*, with *natalensis* A. Smith, 1834 as the valid name, except for *M. kulmei* Setzer, 1956 (not of Thomas & Hinton, 1923) from Darfur Province, Sudan. Petter & Saint Girons (19) retain *M. peregrinus* provisionally as a different species for Morocco. Tranier (26) combined some cranial characters with karyological findings (paired chromosome numbers of 32, 36, or 38) and suggested that *M. peregrinus*, *M. erythroleucus*, and *M. natalensis* are not conspecific. *Mastomys natalensis* should be regarded as a species complex and only intensive research will solve this taxonomic problem.

GENERAL BIOLOGY

The semicommensal habit of *M. natalensis* is mentioned above and is of the greatest importance. Within its distribution range in southern Africa it is commonly found in stacked thorn fences used for cattle enclosures and around cultivated fields; in granaries and store rooms; and in thatch-roofed huts, which normally have walls built of clay-covered poles or sun-dried bricks.

M. natalensis is to some extent dependent on the presence of water, although open water is not necessary. Its distribution in arid areas is restricted to water courses, washes, or pans. It is normally absent from the waterlogged parts of marshes but present in the relatively drier parts and along the edges. It is, for instance, the most abundant species on the Kafue flood plains, just above the water mark (22), and it is found in forest clearings but rare in the forest itself (13, 21).

Although it is an omnivore when a domestic rodent, it is basically gramnivorous and will also eat grass stems and rhizomes. Delany (10) found insect remains in 23 out of 25 stomachs from Uganda.

Its burrowing habit varies remarkably. It utilizes deserted burrows of other rodents, such as gerbils or mole rats, in preference to digging a fresh burrow. Grass stems and leaves are normally used for nesting material. It will form new runways or use existing ones.

It is a nocturnal animal with the peak of activity during the first three hours after darkfall. Choate (3) found that there is an indication of early, middle, and late nightly activity peaks in laboratory mice.

Its climbing ability is such that it is able to climb trees and wall cavities to reach roofs and ceilings; however, it cannot be regarded as a true arboreal species.

Swanepoel (30) studying a small mammal population in an area with extremely low densities, found that the maximum average distance between points of capture is 155 m for male and 81 m for female mice. De Wit (29), used the minimum area method and found that there are also seasonal variations in the home range between males and females. The smallest mean home range was found during the winter of 1970, the spring areas being over 4 times as large for males (mean area 2 666 m^2) and 3 times as large for females (1 833 m^2), with a maximum recorded home range of 4 800 m^2. Hatt (14) recorded homing ability of *Mastomys* up to 300 m.

SOCIAL BEHAVIOUR

Mastomys is gregarious and nests in underground burrows or in protected, dark, hideouts when in human habitations. It may occur in association with other wild rodents, such as *Tatera*, *Rhabdomys*, *Lemniscomys*, *Aethomys*, *Thamnomys*, *Praomys*, and *Mus*, but gives way to *Rattus rattus* pressure. This replacement of *Mastomys* in human habitats occurs commonly in towns and cities; it was also observed, however, along the banks of streams in the eastern Orange Free State.

Veenstra (24) suggests that *Mastomys* is interspecifically and intraspecifically non-aggressive and does not have a strong territorial instinct. Cilliers (28) found that when 5 wild-caught pairs were introduced to a 3.3-m^2 cage a struggle for dominancy was obvious, which resulted in the dominant male killing the 4 other males after continual biting, notwithstanding the fact that submissive behaviour was shown. It was further found that when F_1 males reached subadult stage there was continual sparring, and the male mentioned above slowly lost its dominant position. When this colony, now in a 6.7-m^2 cage, consisted of well over 100 mice, group formation became obvious: (*a*) a dominant group of 6 males and 6 females; (*b*) a large stable group that adapted to cage life and was largely ignored by group (*a*); and (*c*) a group under stress, continually harassed by members of the dominant group, scarred, and most often seen in conflicts (13 conflicts per mouse per hour, as against 5 conflicts per mouse per hour in group (*b*)). Females normally show aggression only before and after births; this changed in the experiment when large numbers were present, and the females of group (*a*) mentioned above showed dominant behaviour equal to that of the males. Males in group (*c*) demonstrated homosexual behaviour. There were indications of territorial behaviour, but it was not properly demonstrated, probably because of the cage size. Cilliers (28) also found that the animals ate small seeds on the spot, holding the seeds in the forepaws, but larger seeds (sunflower) and food pellets they sometimes ate on the spot, sometimes stored in the nest boxes. The food pellets were not lifted to the mouth but held on the ground with the forepaws. Food storage was mainly done by pregnant and nursing females.

Various authors have found that females protect their young and carry them away when the nest is threatened (17); other females and males readily assist the mother in moving her young. Veenstra (24) described locomotion and swimming ability as well as washing, both as a cleaning mechanism and as displacement behaviour.

LIFE CYCLE

The gestation period has been determined as 23 days, with a 25-day interval between litters (7, 18).

The age at first litter can be regarded as 94 days ($\bar{x}$ = 94.1 ± 19.19 days, median 90.25 days and mode 82.5 days (Coetzee, 27)). This means that a female who has young at the onset of the breeding season might give birth to a fourth generation during the 9 to 10 months of the main breeding period. The average litter size can be regarded as 10 on the basis of the mean figures obtained from various parts of Africa, such as Sierra Leone: 11.8 (1), southern Uganda: 12.1 (12), Rukwa, Tanzania: 11.2 (2), southern Malawi: 11.0 (16), Roodepoort, Transvaal: 9.5 (4), and in two different animal room colonies bred from wild stock from the Transvaal: 7.4 and 6.6 (7). Both Hanney (16) and Coetzee (27), found that the litter size is related to the body size of the females.

Coetzee (27), recorded a mean corpora lutea count of 10.92 in a sample of 36 females, 9.47 implanted ova and 9.22 healthy-looking fetuses. A 15.5% loss thus occurs between the number of the ova formed and the number of healthy fetuses. Calculations based on Meester's (17) findings show a 17.3% death rate between birth and weaning age. Hatt (14) quotes figures supplied by D. H. S. Davis (personal communication) for 600 litters that show a 20.8% pre-weaning death rate.

The mean age at death due to natural causes for the two laboratory stocks at the Medical Ecology Centre in Johannesburg is 395 and 487 days (7). De Wit (29) calculated the estimated maximum life-span of free-living Mastomys as 339 days.

POPULATION DYNAMICS

The population structure of a species with a life-span of a year or less is greatly influenced by the breeding period (18). Fig. 1 shows the percentage of pregnant females for the different months of the year for (*a*) Roodepoort and (*b*) northern Botswana (from 23). The relative number of gravid females is compared with the mean monthly rainfall for the different areas. Both the graphs accentuate the low breeding rate during the dry (winter) season. In both cases, a short break in the breeding is noticed during September. Hanney (16) found no gravid animals from June to January 1962 in a sample of 159 females from Malawi. In Uganda, Delany (10) also recorded that there were no pregnant or lactating females from August to December 1961, but Delany & Neal (12) observed pregnant females from May to July and from October to December.

The population structure is also influenced by the relative number of subadults. This depends directly

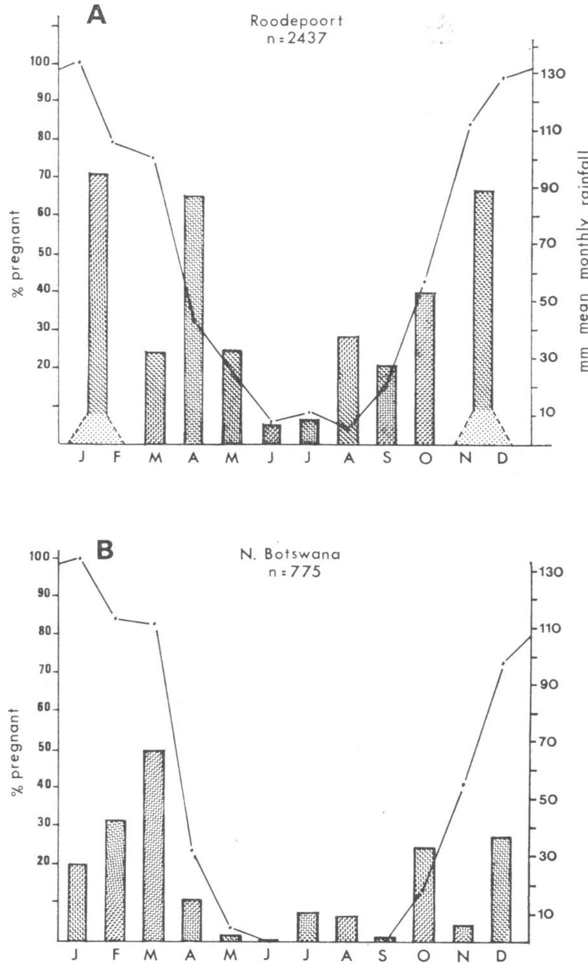

Fig. 1. Percentage of pregnant females of *M. natalensis* from (A) Roodepoort, Transvaal, and (B) northern Botswana as an indication of the breeding season (from Smithers, 23). The mean monthly rainfall is also shown.

on the birth period and on the size of the litters. Fig. 2 (from Coetzee, 27), shows the percentage of juvenile specimens taken at Roodepoort, Transvaal; Lubumbashi, Zaire (Pirlot, 20); Rukwa, Tanzania (Chapman et al., 2); and at Freetown, Sierra Leone (Davis, personal communication). The mean monthly rainfall and temperatures are plotted on the basis suggested by Gaussen (1953, in Walter & Leith, 25), the area of overlap of these climatological factors indicating the so-called " arid " period. The findings shown in Fig. 1 and 2 support the conclusion arrived at by different authors, namely that the peak breed-

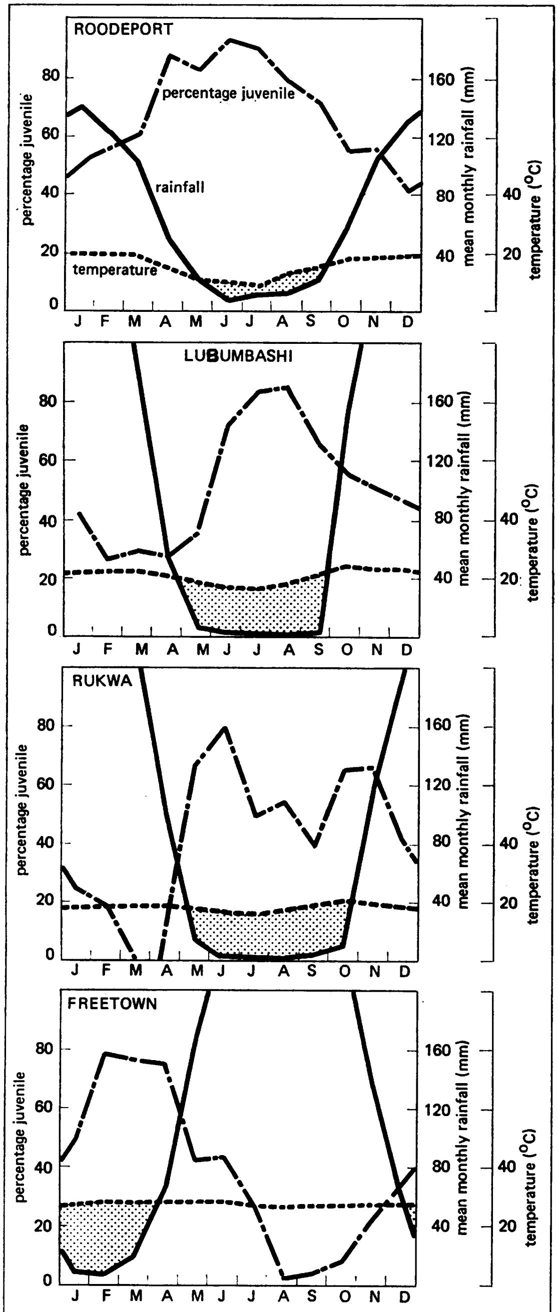

Fig. 2. The breeding pattern of *M. natalensis* as indicated by the percentage of juvenile specimens in relation to the " arid " period, plotted as suggested by Gaussen (in 25), for Roodepoort (Transvaal), Lubumbashi (Zaire), Rukwa (Tanzania), and Freetown (Sierra Leone).

ing season occurs mainly towards the end of the rainy season and beginning of the dry season. However, we cannot ignore the important influence of the differences in the annual rainy pattern found throughout the greater part of Africa.

The two criteria used in demonstrating the seasonal variation in population structure is either body and cranial size (15) or toothwear (6 & 11), or a combination of toothwear and mass (4). Data from Uganda (11) and Roodepoort (4) were used in compiling Fig. 3 to show the variation in seasonal population structure. When animals with a toothwear of II plus in Fig. 3 A and IV plus in Fig. 3 B are regarded as potentially fecund, certain deductions can be made. A larger proportion of the population can be regarded as potential breeders from August to March in case A and during March to May and September to November in case B. Furthermore, in case A, the juveniles (0 toothwear) that form the bulk of the population in January to April, appear again in the toothwear I group about three months later, again as the major group. The same process appears to happen in case B, but on a bi-annual basis. Fig. 3 B shows that the bi-annual addition of young animals to the population can be followed through in the presence of older animals in the following periods. This process of succession is not clearly shown in the toothwear II to VI groups in case A, which supports the idea that a high proportion of the subadults born during autumn in the Transvaal do not survive the winter. This suggests that the cold winters in temperate areas might act as an additional factor in controlling the numbers of *M. natalensis*, a mechanism not present in tropical regions. Such a mechanism would have a direct influence on the spread of diseases, especially if the rodent is a permanent reservoir. The sparser plant cover during the latter part of winter in temperate areas also gives less protection against predators.

Population explosions of *M. natalensis* occur regularly and might be linked with abundance of food (5). The fluctuation in population size is well illustrated by the findings of Chapman et al. (2) in the Rukwa Valley of Tanzania, where unbaited petrol drums were used as traps in grain stores. The average daily catch during July 1956 was 1938 mice, compared with only 36 in November of that year and with 33 during November of the previous year at a nearby store. During years of population explosion, the mice form the main diet of predators and thereby protect other less common species from predator pressure.

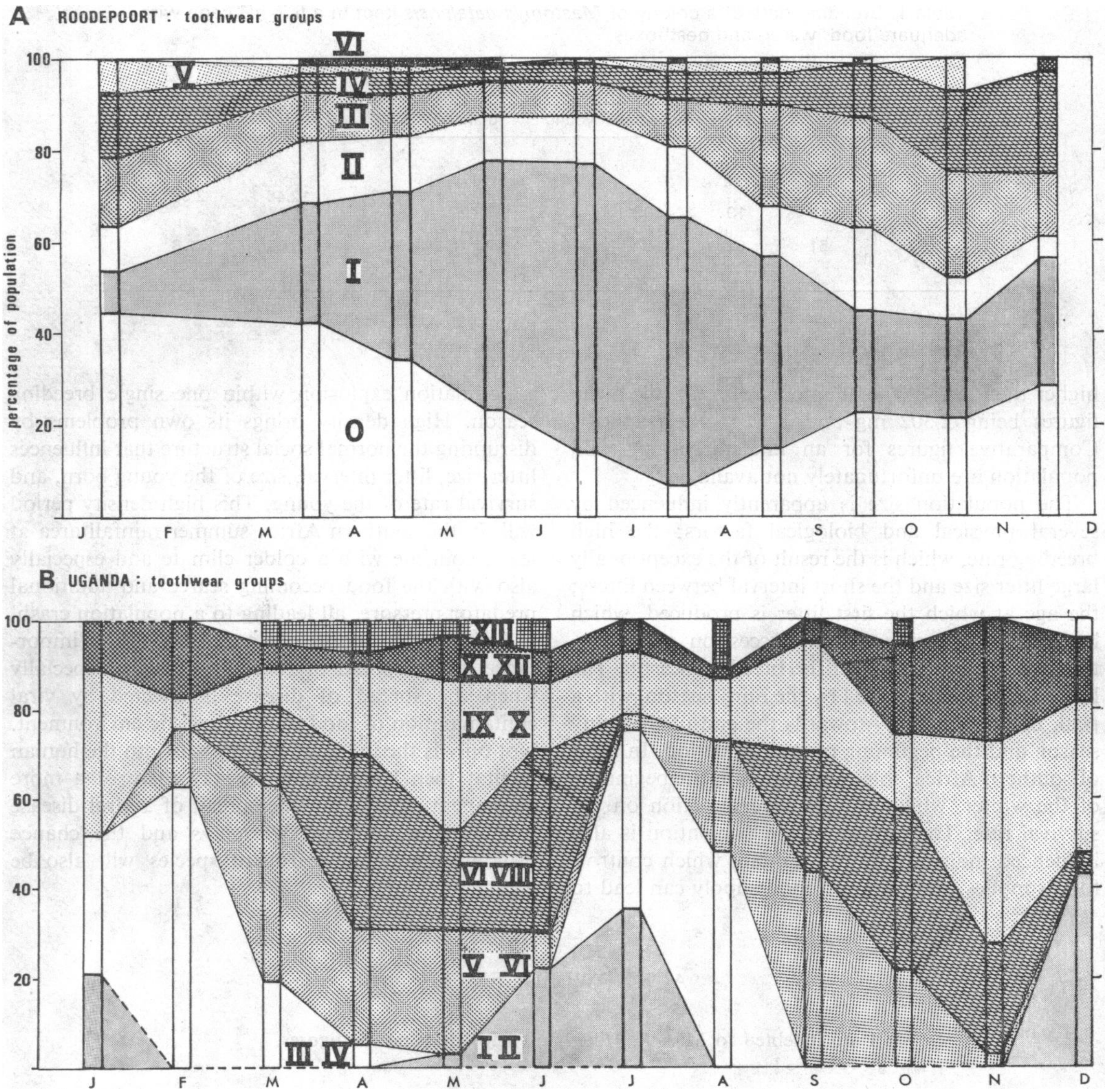

Fig. 3. The age distribution of *M. natalensis*. A—from Roodepoort, Transvaal, based on a combination of toothwear classes and body mass. B—from Uganda based on toothwear classes (from data in Delany, 11).

The natural regulation of rodent populations during periods of high density still needs intensive study. Cilliers (28), when observing population growth in a *Mastomys* colony kept in a 6.7-m² enclosure, was able to distinguish clearly between the breeding potential during the period of growth of the colony and that when population pressure became obvious. His findings are given in Table 1, which clearly demonstrates that the breeding rate is affected by a prolonged litter interval, the litter size being greatly reduced and the young being considerably smaller. The young born during this period were all killed, the females exhibiting a lack of interest in them.

Cilliers also found that the adrenal mass of the mice of the dominant and submissive groups (see groups (*a*) and (*c*) above under *Social behaviour*) was

Table 1. Breeding data of a colony of *Mastomys natalensis* kept in a 6.7-m^2 cage with adequate food, water, and nestboxes.[a]

Period (weeks)	Colony size					Mean number of litters	Mean litter size	Mean mass at birth (g)
	♂♂	♀♀	subadult	young	total			
0	2	4	—	4	10	0.65	12.46	2.38
21	12	19	60	61	152			
32	51	62	3	0	116	0.25	5.06	1.8

[a] Based on Cilliers (28).

higher than that of the adapted group (*b*), the mean figures being 2.302 mg and 1.32 mg respectively. Comparative figures for an undisturbed or wild population are unfortunately not available.

The population size is apparently influenced by several physical and biological factors: the high breeding rate, which is the result of the exceptionally large litter size and the short interval between litters; the age at which the first litter is produced, which has a direct bearing on the succession of generations; and the duration of the breeding season. The latter is largely controlled by the rainy season, with a peak breeding activity towards the end of the rainy season and the beginning of the dry period. In most of southern Africa, this coincides with the beginning of the winter, which has an adverse action on the survival rate. The growth of the population is also influenced indirectly by the rainfall, which controls food supplies. An optimum food supply can lead to a population explosion within one single breeding season. High density brings its own problems by disrupting the normal social structure that influences litter size, litter interval, size of the young born, and survival rate of the young. This high density period will, in the southern Africa summer rainfall area at least, coincide with a colder climate and especially also with the food becoming scarce and additional predator pressure, all leading to a population crash.

The high density periods are of the utmost importance in the spread of zoonotic diseases, especially when the spread of disease is effected by viral contamination of food in the domestic environment. Not only is the influx of the animals into the human habitat then larger, and the stay there of a more permanent nature, but the spread of a viral disease will increase amongst *Mastomys* and the chance of contact with other rodent species will also be greater.

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RÉSUMÉ

BIOLOGIE, COMPORTEMENT ET ÉCOLOGIE DE *MASTOMYS NATALENSIS* EN AFRIQUE MÉRIDIONALE

Le rat du Natal (*Mastomys natalensis*) vit dans la plupart des régions d'Afrique, à l'exception des déserts (précipitations annuelles inférieures à 200 mm), de la plus grande partie du bassin du Zaïre et des régions à pluies hivernales typiques. Il est semi-commensal de l'homme sur toute son aire de répartition et peut être, dans certains cas, considéré comme un véritable rongeur domestique. C'est une espèce nocturne. Principalement granivore et grégaire, l'espèce vit en association avec d'autres, mais elle se retire en présence du rat *Rattus rattus*. Le territoire du mâle s'étend sur plus de 110 m et celui de la femelle sur plus de 70 m; ce facteur joue un rôle important dans la dispersion de l'espèce et dans la détermination de la distance entre l'endroit où *Mastomys* installe son terrier et l'habitation humaine où il trouve sa nourriture. C'est un animal social, à système

hiérarchique normal. L'assistance mutuelle pratiquée au sein du groupe familial assure un taux de survie assez élevé. Dans les périodes de reproduction normale, une portée de dix petits peut être considérée comme moyenne; l'intervalle moyen entre les portées est de 23 jours et les femelles ont leur première portée à l'âge de 94 jours. L'espérance de vie de l'espèce est d'environ un an. La reproduction est généralement maximale à la fin de la saison des pluies et au début de la saison sèche. Dans les régions caractérisées par des précipitations estivales suivies par un hiver froid, le nombre des petits est fortement réduit à cause du surcroît de stress dû aux températures nocturnes plus basses, de l'action des prédateurs et de la moindre quantité de nourriture disponible. La distribution de la population de *Mastomys* est indiquée pour le Transvaal et le sud de l'Ouganda. L'espèce est sujette à des explosions de population qu'on peut partiellement attribuer à l'abondance de nourriture. Durant les périodes de forte densité, on peut observer un comportement social anormal et des symptômes de stress tels qu'une plus grande fréquence des conflits et une augmentation de volume des glandes surrénales. Cette situation aboutit à une désorganisation complète de la reproduction. La semi-commensalité, associée au taux de reproduction élevé, avec de fréquentes explosions de population, constitue un facteur idéal de propagation des maladies entre animaux sauvages et animaux domestiques.

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